Giving Up Density as an approach to identify a difference in foraging behavior between native and invasive crayfish species

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Abstract:

Invasive species are often thought to displace native species by being superior competitors through aggression and resource exploitation. In freshwater ecosystems, invasive crayfish have been frequently shown to displace native crayfish by outcompeting them for food resources. Here, we tested the hypothesis that the displacement of native crayfish, *Orconectes sanbornii*, by invasive crayfish, *Orconectes rusticus*, in Ohio streams may be due to superior foraging behavior of the invader. We also examined whether foraging behavior changed in the presence of a model fish predator. We ran a lab experiment where we used depletable food patches to compare the foraging behavior of native *O. sanbornii* and invasive and native populations of *O. rusticus* under high, low or no predation risk. The amount of food remaining in a patch after approximately a 24-hour period was used as an indication of giving up density (GUD) to measure crayfish foraging behavior under predation risk. Results indicated that there was no effect of predation risk on the GUD of either species ($F_{2,80} = 0.147$, $p = 0.86$). However, native *O. sanbornii* left lower GUDs on average than either native or invasive populations of *O. rusticus* ($p = 0.003$, $p = 0.026$, respectively). This suggests that the native *O. sanbornii* is a more active forager than either a native or invasive population of *O. rusticus*. This suggests that *O. rusticus* might not be displacing *O. sanbornii* through exploitative competition but rather an unidentified mechanism. Gaining a better understanding and being able to better identify the mechanisms of species invasions can lead to better and more effective management of invasive species in the future.

Introduction:

Invasive species are often thought to displace native species by being superior competitors through traits like aggression and resource exploitation. Displacement by invasive species can reduce populations of native species and can greatly affect community structure (Pintor & Sih, 2009). The range of *O. sanbornii* used to stretch to west-central Ohio but due to *O. rusticus* invasion and expansion of their range, *O. sanbornii* has been extirpated from their original range and only reaches as far west as the Licking River system, which is east of central Ohio (Butler & Stein, 1985). Concentrations of *O. sanbornii* in the Licking River system have also been shown to decrease in the Licking River system since the introduction of *O. rusticus* (Jezerinac, 1991). Which can be an indication that *O. rusticus* is still displacing *O. sanbornii* even farther. *O. rusticus* is known to replace several different species of crayfish across north-central and northeastern North America and be successful in multiple different types of habitat (Butler, 1988). Studies have shown that *O. rusticus* invasions can have large effects on the entire ecosystem (Reid & Nocera, 2015) (Wilson et al., 2004). For example, Wilson (2004), found in a temperate lake, in Wisconsin, that after *O. rusticus* invaded and was established there was a large decrease in fishes that share prey taxa with crayfish, snails decreased from >10 000 to <5 snails*m^2 and there were changes in the population make up of aquatic invertebrates.

We compared the foraging behavior of a crayfish (*Orconectes rusticus*) from its native and invasive ranges and a native crayfish (*Orconectes sanbornii*) species in Ohio using a Giving Up Density (GUD) approach. For prey species, like crayfish, foraging behaviors require time, energy and exposure to predation risk (Brown & Kotler, 2004). GUD is an approach that measures the amount of food remaining in a depletable food patch after a specified amount of time (Bedoya-Perez et al., 2013). By measuring the density of the remaining food after an individual has completed foraging, the individual's foraging activity can be quantified. Individuals that leave a high density of food behind will have a higher GUD, which signifies that individual is not a very active forager. When an individual leaves a low density of food behind they will have a low GUD density, which can indicate a low amount of foraging activity. When compared between species, GUDs can indicate which species is a more active forager. Being a more active forager indicates and individuals willingness to take on risk to forage more (Bedoya-Perez et al., 2013). Between two competing species, the species that is more capable of exploiting the resources available in a food patch will likely be the more successful species. This is because the species is outcompeting the other for resources and the individuals that receive the most resources will likely be able to grow and reproduce more and have higher energy which can lead to improved success.

Methodology

Crayfish used in this experiment were collected from three different sites. The first site, the farthest west, was where the *O. rusticus* population that was in their native range were collected (Figures 1 & 2). The second site, in the middle, was where the *O. rusticus* population that was considered invasive were collected. The last, farthest east site, was where the native *O. sanbornii* population was collected. All populations were collected from streams where the other species was absent, so there were only *O. sanbornii* or *O. rusticus* in each site.

An individual crayfish was placed in a 35.38"L x 16.75"W x 5.88"H arena that contained a PVC shelter and a depletable food patch on opposite ends of the arena (Figure 3). The crayfish were left in the arenas for approximately 24hours and were either subjected to no, low or high predation risk. Predation was simulated using a model fish predator, a small mouth bass. If the crayfish was in shelter, then the model fish predator was presented to the crayfish to ensure the crayfish knew there was predation risk. If the crayfish was out of shelter or actively foraging, the model fish predator was used to chase the crayfish back into shelter.

The depletable food patches consisted of a circular plastic bowl, 12" in diameter, filled with crushed brick and chicken liver. At the start of each trial the depletable food patch was loaded with about 0.80 grams of chicken liver that was hidden in the crushed bricks. After the 24hour trial was completed the remaining food was retrieved and weighed to obtain the change in mass of chicken liver, or food consumed value. Dry mass was used to measure the mass of chicken liver for accuracy, due to the wet environment and small measurements being taken. Each treatment combinations (population x predation risk) was replicated 10 times.

GUD has some limitations that can complicate the results, but some can be addressed through experimental design. The limitations of GUD experiments include, the curvilinearity between harvest rate and energy, the energetic state of the forager, the effect of group foraging, food quality and substrate properties, the predictability of the food patch, behavioral traits of the forager and nontarget species (Bedoya-Perez, 2013). The limitations that were addressed in our experimental design include, the energetic state of the forager and food quality and substrate properties (Bedoya-Perez et al., 2013). By doing the experiments in the laboratory it was possible to control the energetic state of the forager through feeding and isolating the forager before trials. Food quality and substrate properties were addressed by putting the same food in the depletable foraging patches throughout the entire experiment and by using the same substrate throughout and also experimenting with other crayfish to ensure they can forage in that substrate. The effect of group foraging was not included in this experiment because all the trials were done with one solitary crayfish and crayfish are typically not a social forager (Browne & Moore, 2014). Crayfish rely heavily on olfactory cues in their foraging activities instead of group foraging activities (Browne & Moore, 2014). The predictability of the food patches was not considered in this experiment because trials were done once, in a 24-hour period so there was not enough time nor were the crayfish exposed multiple times to learn about the predictability of the food patch. Finally, nontarget species were not included in this experiment because it was done in a laboratory outside of the effects of nontarget species.

Results and Analysis

Results indicated that there was no effect of predation risk on the amount of food consumed by any population ($F_{2,80} = 0.147$, $p = 0.86$) (Figures 4 & 5).

Native *O. sanbornii* consumed a significant amount of food more than either population of *O. rusticus* (native *O. rusticus*, $p = 0.003$, invasive *O. rusticus*, $p = 0.0256$) (Figure 6).

This experiment was conducted over two years. Therefore, we included year in our statistical model. Although there was a significant effect of year ($p < 0.001$), there was still a significant difference between the foraging activity of *O. rusticus* and *O. sanbornii* even when year was accounted for ($p = 0.004$) (Figure 7).

The analyses were completed using the metrics of the dry mass of the amount of food consumed by each crayfish, crayfish mass, populations and year. We used the dry mass of the amount of food consumed to indicate GUD. Because all individuals started trials with the same initial mass of food, the amount of food consumed is indicative of GUD. This is because when a crayfish eats more food they leave behind a lower density of food, indicating a lower GUD and vice versa. The amount of food that was consumed was divided by the mass of that individual crayfish to account for the crayfish's size. This was the response variable. The populations (native *O. sanbornii,* native *O. rusticus* and invasive *O. rusticus*) were the independent variable and year was a covariate.

Discussion & Conclusion

The results indicated that there was no effect of predation risk on crayfish foraging activity and that *O. sanbornii* has a lower giving up density than *O. rusticus*. This is the opposite result of our original hypothesis, but these results are still supported in the literature. There are multiple hypothesis that could explain these results. Further research will need to be conducted to be able to apply different hypothesis to this experiment.

There was no effect of predation risk observed on crayfish foraging activity in this experiment. This is likely due to the predator model not being thorough enough. Crayfish have a strong sense of smell and rely heavily on olfactory cues (Browne & Moore, 2014). It is likely that physical and visual cues of a predator were not enough to elicit a response from the crayfish. Adding the scent of a predator species, like a small mouth bass, or the scent of other crayfish, either under stress or deceased, would have likely elicited a response from the crayfish in the experiment.

Our result, that *O. rusticus* is a less active forager than *O. sanbornii*, is supported by Brown & Kotler, 2004, stating that foragers with a higher energy state or survivor's fitness will have higher GUDs. Meaning that, in this case, the more fit individual will consume less food, even though they are the ones replacing the other species. Also, the individual that has a higher energy state or survivor's fitness can afford to forage less often (Brown & Kotler, 2004). In terms of GUD the more fit individual will leave more food behind meaning they will have a higher GUD. In this study, it is possible that the *O. rusticus* were able to hold out for longer than the *O. sanbornii* and the trials were only 24hours long so the trials may not have been able to account for that. In this study the more fit individual is thought to be *O. rusticus* due to their ability to invade habitats and replace crayfish species within them (Hill & Lodge, 1999).

A different hypothesis that could explain these results would be that *O. rusticus* is superior at obtaining shelter or is taking shelter from *O. sanbornii* (Savvides & Louca, 2015). This hypothesis cites the interaction between a crayfish and a crab species where the two species would often fight each other over shelter and the winner receives the shelter (Savvides & Louca, 2015). The idea here is that *O. rusticus* may have a stronger strategy of obtaining food and shelter from other individuals rather than foraging for food outside of shelter. Rather than spending their time and energy on foraging activities that are far from shelter and what is familiar to the individual, *O. rusticus* may employ a strategy of seeking out other crayfish or similar individuals and take food and resources from them.

Further research that could be conducted to try and explain these results could be a physiological study of *O. rusticus* and *O. sanbornii.* This could be monitoring metabolic rates and growth rates of the two species. If one species has a physiological advantage over the other than it will help decide which species has the higher survivor's fitness and energy state. If *O. rusticus* has the physiological advantage than it supports these results and the hypothesis by Brown & Kotler, 2004. Also, further experiments should include interactions between *O. rusticus* and *O. sanbornii.* By observing the interactions between the two species one can quantify the agonistic behavior of the individuals. If *O. rusticus* is more agonistic and takes shelter away from *O. sanbornii* than it supports Savvides & Louca, 2015 hypothesis. This hypothesis could be taken a step further to see if the species will fight each other for food and if one species dominates the other.

The results of this experiment indicate that *O. sanbornii* is a more active forager than *O. rusticus.* Since it was the opposite result of our hypothesis this opened the experiment to future research and alternate hypotheses. Some of these hypotheses include physiological differences between the species and effects of the interactions between the two species, and future experiments should focus on the interactions *O. rusticus* has with other species.

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Appendix

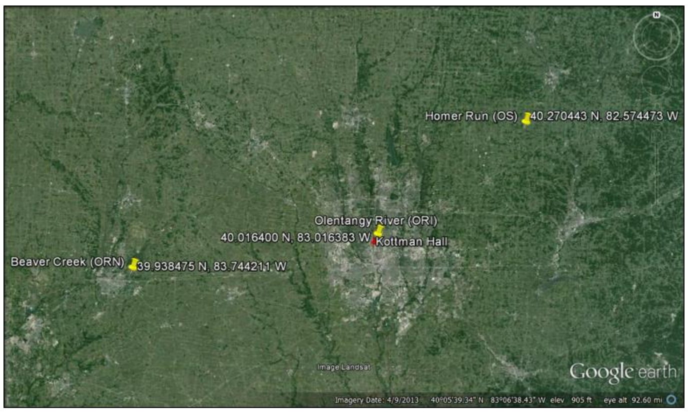

Figure 1: Map of all sites where crayfish populations were collected from. The site labeled "Beaver Creek (ORN)" was where the native *O. rusticus* population was collected. The site labeled "Olentangy River (ORI)" was where the invasive *O. rusticus* population was collected. Finally, the site labeled "Homer Run (OS)" was where the native *O. sanbornii* population was collected.

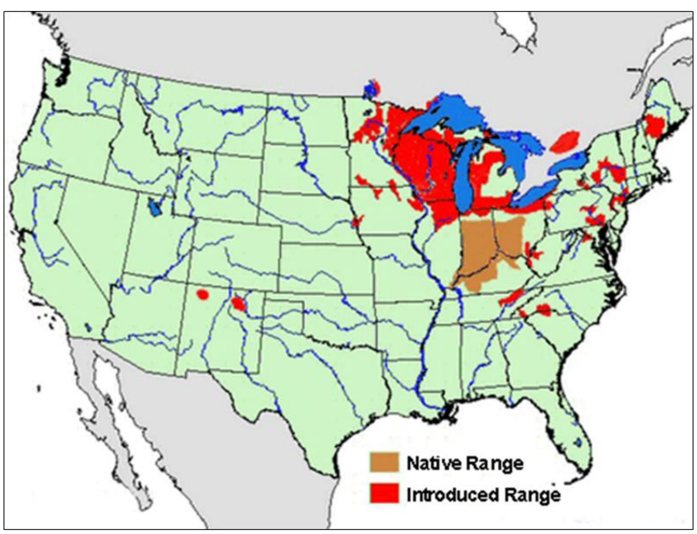

Figure 2: Map of the native and introduced ranges of *Orconectes Rusticus*. http://www.seagrant.umn.edu/ais/rustycrayfish_invader

Figure 3: A representation of the experimental design. The triangle represents the PVC shelter and the black circle is the depletable foraging patch, a 12” in diameter plastic bowl that was filled with brick chunks and chicken liver. The arena measures, 35.38"L x 16.75"W x 5.88"H.

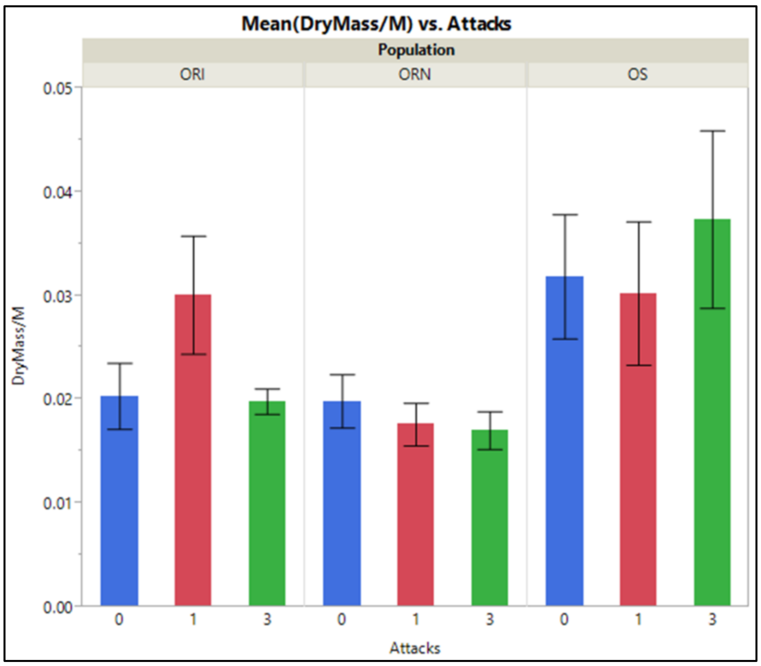

Figure 4: Mean food consumed divided by mass of crayfish separated into predation risk and populations. Predation risk is on the bottom x-axis, labeled attacks. Mean food consumed, divided by mass of crayfish is on the y-axis. This is the response variable that is indicative of GUD. The populations are on the top x-axis. “ORI” signifies the invasive population of *O. rusticus*. “ORN” signifies the native population of *O. rusticus*. “OS” signifies the native population of *O. sanbornii*. No significant results were found here.

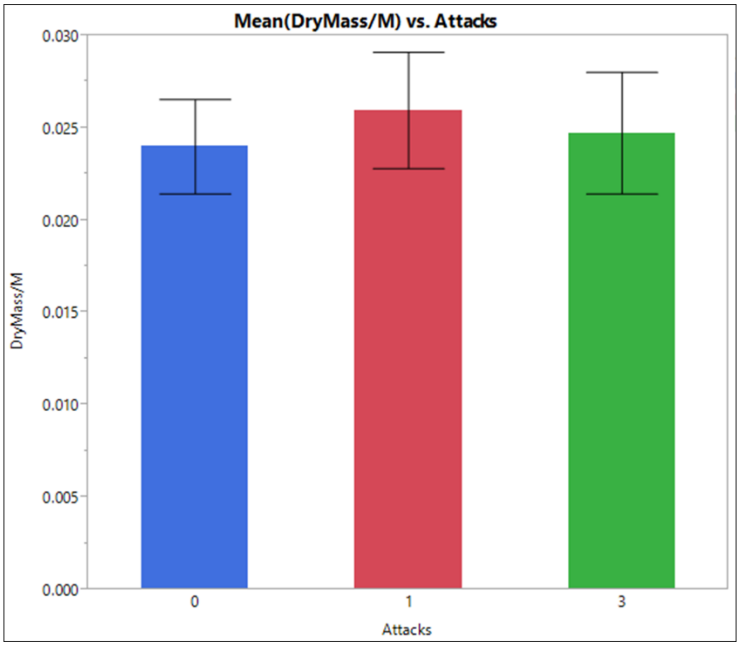

Figure 5: Mean food consumed divided by mass of crayfish separated into zero, low and high predation risk (Attacks). No significant results were found here.

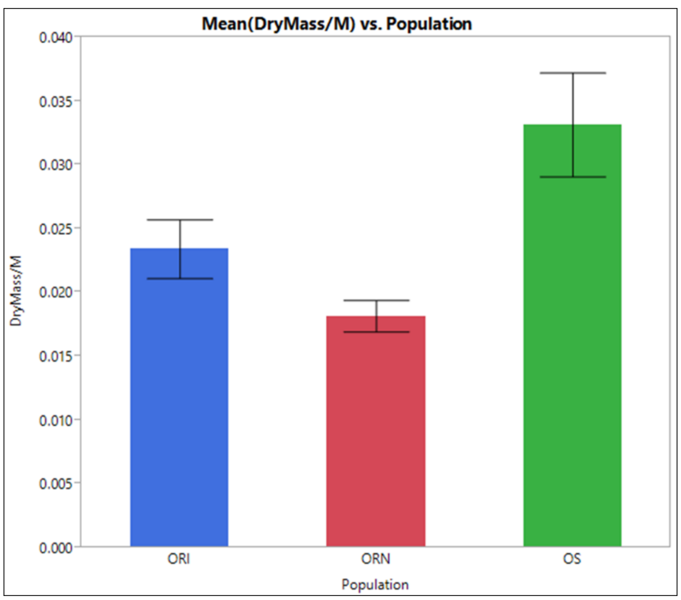

Figure 6: Mean mass of food consumed divided by the mass of crayfish per population with standard error bars. “ORI” signifies the invasive population of *O. rusticus*. “ORN” signifies the native population of *O. rusticus*. “OS” signifies the native population of *O. sanbornii*. There was a significant difference between *O. sanbornii* and both populations of *O. rusticus*.

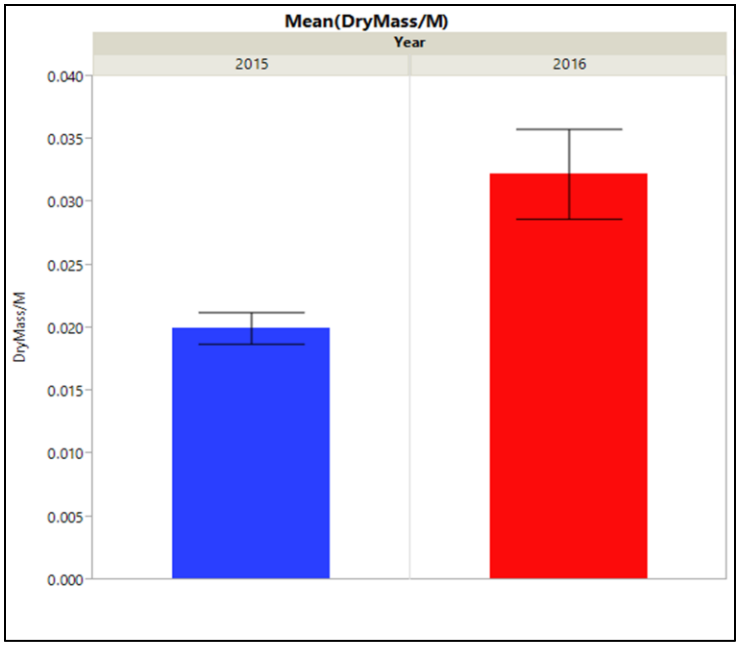

Figure 7: Mean food consumed divided by crayfish mass separated into the years the experiments were conducted. There was a significant result found here, but when accounted for in the model the species interactions were still the same and significant.